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Chlorophyll fluorescence and "Maximum Quantum Efficiency" of photosystem II in plant sciences

Y.M. Feyziyev*

*Institute of Molecular Biology & Biotechnologies, Azerbaijan National Academy of Sciences, 11 Izzat Nabiyev, Baku AZ 1073, Azerbaijan; *For correspondence: y.feyziyev@imbb.science.az*
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The fluorescence of chlorophyll *a* is widely used as an indicator of the state of photosystem II (PSII) in plants, algae and cyanobacteria. There were reports on ~ 20 various parameters of fluorescence of PSII chlorophyll. Three of these characteristics, the initial (F_0), maximum (F_M) and variable (F_V) fluorescence of chlorophyll, and the derivative value (F_M-F_0)/F_M, called by different authors a "maximum quantum efficiency" of PSII, are reviewed in this paper. A brief and comparative analysis of the Duysens hypothesis (Duysens and Sweers, 1963) and Klimov's hypothesis of recombination luminescence (Klimov et al., 1978) widely used to describe the processes in the PSII reaction center was carried out. Eventual errors due to inaccuracy in the applications of the parameter "maximum quantum efficiency" of PSII used to evaluate the photochemical activity of the photosynthetic apparatus and the physiological state of plants are discussed.

Keywords: *Photosystem II, chlorophyll fluorescence, maximum quantum efficiency*

Abbreviations:

Chl – Chlorophyll; **CP43, CP47 –** 43 and 47 kDa PSII core antenna proteins, Chl *a* proteins; **Cyt b_6f –** Cytochrome b_6f complex; **D_1, D_2 –** PSII reaction center proteins; **F_0, F_M, F_V –** Initial, maximal and variable fluorescence of Chl *a*; **k_f, k_d, k_e –** Rate constants of fluorescence, thermal dissipation and photochemical quenching, respectively; **LHCII –** Light harvesting complex II; **$NADP^+$ –** Nikotinamide-adenine dinucleotide phosphate, oxidized; **Q_A –** Plastoquinone, primary electron acceptor of PSII, $Q_A^{-\bullet}$ (semiquinone) reduced form; **Q_B –** Plastoquinone, secondary electron acceptor of PSII; **Pheo –**Pheophytin, $Pheo^{-\bullet}$ reduced form; **P_{680} –** Primary electron donor, P_{680}* and $P_{680}^{+\bullet}$ excited and oxidised forms; **PQH_2 –** Plastoquinole; **PSI, PSII –** Photosystem I, Photosystem II; **RC –** Reaction center; **Y –**"Maximum quantum efficiency" of photosystem II, (F_M-F_0)/F_M; **Y_Z, Y_D –** Redox active tyrosines of PSII: Y_Z is a redox intermediate between PSII reaction center and water oxidation; **φ_f, φ_d, φ_p –** Quantum yield of fluorescence, thermal dissipation and photochemistry.

INTRODUCTION

The photosynthetic apparatus of oxygen-evolving species converting light energy to the chemical energy of organic compounds includes several protein complexes located in the thylakoid membrane. These are complexes: photosystem I and II (PSI and PSII), cytochrome b_6 *f* (Cyt b_6 *f*), ATP-synthase and $NADP^+$. A combined action of the photosystem II and I results in the electron transfer through the thylakoid membrane, from H_2O ($E_{m\ (pH\ 7.0)}$ = +0.82 V) to $NADP^+$ ($E_{m\ (pH\ 7.0)}$ = –0.32 V), using two light quanta (one for each photosystem) for the transfer of each electron. In the redox potential scale, the photosynthetic electron transfer is represented by the Z-scheme of photosynthesis in which the photochemical reactions of PSII and PSI interact through the electron transfer chain consisting of the pool of plastoquinols (PQH_2), Cyt b_6 *f* and plastocyanin (Hill, 1965; Govindjee et al., 2017).

The photosystem II of oxygenic organisms couples the photochemical excitation of chlorophyll with the electron transfer from water to PQH_2. Stu-

dies of the molecular architecture of PSII in cyanobacteria and red algae have revealed ~20 proteins and a number of cofactors in the structure of this complex (Zouni et al., 2001; Ferreira et al., 2004; Umena et al., 2011, Ago et al., 2016). The transmembrane D_1 and D_2 proteins (32-34 kDa), α- and β-subunits of cytochrome b_{559}, core antenna proteins CP47 and CP43 carrying Chl *a*, and three peripheral proteins of 33-, 23- and17 kDa located on the lumen surface of thylakoid membranes are the most important proteins of photosystem II in plants. Cyanobacteria and red algae contain cytochrome c_{550} and 12 kDa PsbU polypeptide, instead of plant 23 and 17 kDa polypeptides.

D_1/D_2 heterodimer of the PSII complex binds an initial electron donor P_{680}, pheophytin (Pheo) and two plastoquinones (plastoquinone O_A and Q_B) electron acceptors, two redox active tyrosines Y_Z (D_1-Tyr^{161}) and Y_D (D_2-Tyr^{161}) as an electron donor to the photooxidized P_{680} (Barber, 2006; Muh and Zouni, 2011). During excitation, P_{680} oxidizes and the electron is transferred to the pheophytin molecule, resulting in the formation of oxidized $P_{680}^{+\bullet}$ and reduced $Pheo^{-\bullet}$ radicals (Klimov et al., 1977) in the PSII reaction center (RC). The quantum yield of charge separation in the PSII reaction center is ~1.0 (Groot et al., 1997). From $Pheo^{-\bullet}$ the electron is transferred sequentially to plastoquinones Q_A and Q_B, and then to the pool of plastoquinols, which serves as a reservoir for electrons leaving PSII. The oxidized primary donor of photosystem II, $P_{680}^{+\bullet}$ is a strong oxidant (E_m ~ 1.2 V) which is reduced by an electron transferred from tyrosine Y_Z. This leads to the oxidation of tyrosine Y_Z and forming $Y_Z^{+\bullet}$ radical. Oxidized tyrosine ($Y_Z^{+\bullet}$) is ultimately reduced by an electron from water (Debus, 1992; Nelson and Yocum, 2006; Muh and Zouni, 2011).

Among the components of the photosynthetic apparatus, PSII is a most sensitive to the extreme factors, and therefore, the characteristic reactions of PSII including the fluorescence of chlorophyll *a* are attracted to research as an indicator the physiological state of oxygenic species. About 20 components of chl *a* fluorescence, applied to the study of oxygenic photosynthesis, are described in different studies. However, most of the components of chlorophyll *a* fluorescence are not characterized sufficiently, that does not allow determining the state of PSII adequately.

In this paper the constant and variable components of chlorophyll fluorescence (F_0 and F_V, respectively), as well as the derivative parameter called the "maximum quantum efficiency" of PSII designated as Y have been considered briefly in the context of their correct interpretation in studies of photosynthesis and various problems of plant science.

2. The fluorescence of chlorophyll a

Photosynthesis starts with the absorption of light quanta by the antenna pigments. A small part of the absorbed light energy (~ 2%) is not used in photosynthesis and lost as a fluorescence of chlorophyll. At room temperatures, fluorescence emitted by chloroplasts and thylakoid membranes has a major band with a maximum at 685 nm and a non-intense broad band (≤ 10% of total intensity) in the red spectral region extending up to 760 nm. At low temperatures (77 K), three emission bands with maxima at 685, 695 and 735 nm are resolved. It is assumed that the 685 and 695 nm bands are emitted by the PSII components, and the 735-nm band is associated with photosystem I (Briantais et al., 1986).

The intensity of PSII chlorophyll fluorescence is sensitive to the redox state of its components. Depending on the redox state of the PSII electron transport chain, several components are distinguished in the yield of chlorophyll fluorescence of oxygenic species. Among them, the most interesting are the parameters such as the "initial" (F_0) and "variable" fluorescence of chlorophyll (F_V), and the "maximum quantum efficiency" of photosystem II (Y), widely used by researchers as a tool in monitoring the physiological state of plants. The use of fluorescence in studies of oxygenic species is well reviewed in several articles (Krause and Weis, 1984, 1991, Horton and Bowyer, 1990; Campbell et al., 1998; Lazar, 1999; Maxwell and Johnson, 2000; Baker, 2008; Brestic and Zivcak, 2013; Kalaji et al., 2014, 2016; Goltsev et al., 2019).

2.1. The initial fluorescence of chlorophyll, F_0

The initial fluorescence of chlorophyll F_0, often referred as a constant, zero or prompt fluorescence, can be observed when the primary electron acceptor of the photosystem II plastoquinone Q_A is in the oxidized state and the PSII reaction cen-

ters are "open". In this state, the yield of chlorophyll fluorescence is minimal. F_0 can be observed under a weak measuring light (which prevents the accumulation of Q_A in the reduced state) in photosynthetic organelles or the suspensions containing PSII (in leaves, chloroplasts, plant thylakoid membranes, green algae and cyanobacteria) after prolonged dark adaptation.

F_0 represents the radiative deactivation of the excited state of antenna chlorophylls during the energy transfer to the PSII reaction centers, i.e. loss of the part of the excitation energy before it reaches the RC (Fig. 1, a). The fluorescence of the chlorophyll of photosystem I (> 700 nm) can also contribute to F_0. However, at a wavelength < 700 nm this contribution is negligible (Schreiber et al., 1998) and may not be taken into account. The lifetime of chlorophyll fluorescence determined by time-resolved fluorometry in dark adapted and quinone oxidized samples shows the decay components in the range of few hundred picoseconds which attributed to F_0 (Haehnel et al., 1982; 1983; Nairn et al., 1982; Karukstis and Sauer, 1985; Mauzerall, 1985; Holzwarth et al., 1985; Moya et al., 1986; Hozwarth, 1986).

2.2. Variable fluorescence of chlorophyll, F_V

When the primary electron acceptor of photosystem II, plastoquinone Q_A, is reduced (photochemically, under strong excitation light, or chemically, for example, in the presence of dithionite), the intensity of chlorophyll fluorescence increases 4-5-fold, from the initial F_0 level to the maximum F_M (Klimov et al., 1977). The state of RC when Q_A becomes reduced is often referred as a "closed" state of PSII, although such terminology is not quite true (see section 2.3). The difference $F_V = F_M – F_0$ is called the variable fluorescence of chlorophyll. Variable fluorescence of chlorophyll is observable in plant leaves, chloroplasts, thylakoid membranes, enriched with PSII complexes, as well as in cyanobacteria and algae. It is intensively used in the study of the photosynthetic apparatus and physiological state of the oxygenic species. Below we will compare two different views of the mechanism of increasing chlorophyll *a* fluorescence, proposed by Duysens and Sweers (1963), and Klimov et al. (1977).

Duysens and Sweers (1963). The hypothesis of Duysens and Sweers (1963) explains the increase of the fluorescence intensity due to blockage of the photochemical quenching of the excited chlorophyll molecules of the light-harvesting antenna after the reduction of plastoquinone Q_A. According to this hypothesis, the quantum yields of fluorescence for "open" (φ_0) and "closed" (φ_m) reaction centers may be determined as follows:

$$\varphi_0 = \frac{k_f}{k_f + k_d + k_p} \quad (1)$$

$$\varphi_m = \frac{k_f}{k_f + k_p} \quad (2)$$

where k_f, k_d and k_p are the rate constants of fluorescence, radiationless transition to the ground state, and photochemical quenching (photochemical electron transfer), respectively.
Simple calculations using equations 1 and 2, and the relation,

$$\varphi_p + \varphi_d + \varphi_f = 1$$

which includes the quantum yields of three basic processes involved in the utilization of the energy of the absorbed light quanta, photochemistry (φ_p), thermal dissipation (φ_d) and fluorescence (φ_f), give the following result for the quantum yield of photochemistry (Borisov and Godik, 1973):

$$\varphi_p = 1 - \frac{\varphi_0}{\varphi_m} \quad (3a)$$

Considering the proportionality of the fluorescence intensity (F) and its quantum yield ($F \propto \varphi_f$), the last equation can be expressed as:

$$\varphi_p = 1 - \frac{F_0}{F_M} \quad (3b)$$

Equations (3a) and (3b) are easily transformed into the following equivalent equations:

$$\frac{\varphi_m}{\varphi_0} = \frac{1}{1 - \varphi_p} \quad (4a)$$

$$\frac{F_M}{F_0} = \frac{1}{1 - \varphi_p} \quad (4b)$$

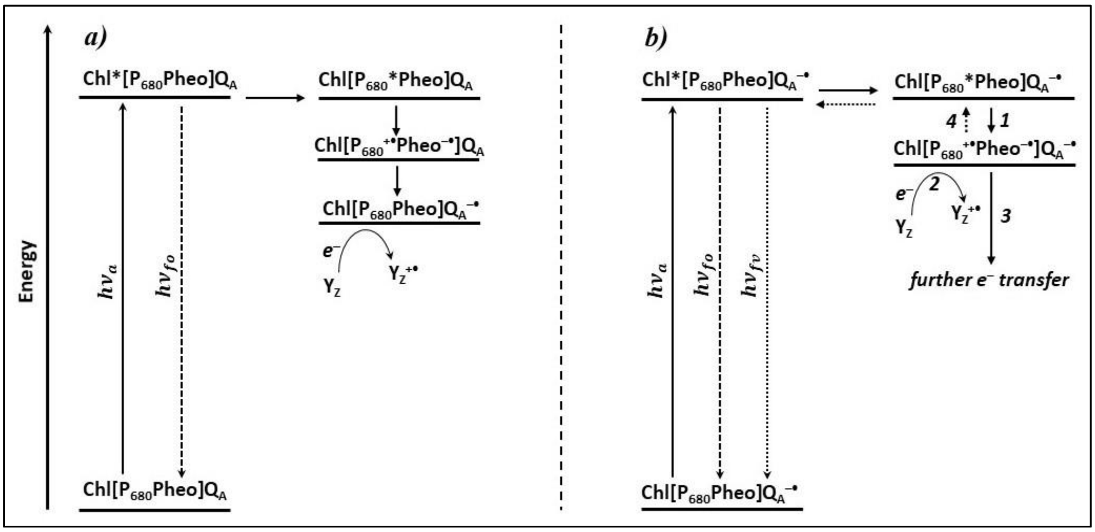


Figure 1. a) – Appearance of prompt fluorescence. b) – Appearance of variable fluorescence of chlorophyll by the mechanism of recombination luminescence (Klimov et al., 1978): $h\nu_a$ - absorption of light quantum, $h\nu_{f_0}$, $h\nu_{f_v}$ - emission of initial and variable fluorescence, respectively. The states of $[P_{680}^{+\bullet}Pheo^{-\bullet}]Q_A^{-\bullet}$ (scheme b) can be stabilized in two ways: 1) electron transfer from Y_Z to $P_{680}^{+\bullet}$: $Y_ZP_{680}^{+\bullet} \rightarrow Y_Z^{+\bullet}P_{680}$ (transition 2), and from pheophytin to plastoquinones: $Pheo^{-\bullet}Q_A^{-\bullet}Q_B \rightarrow PheoQ_A^{-\bullet}Q_B^{-\bullet}$ (transition 3); 2) recombination of the pair $[P_{680}^{+\bullet}Pheo^{-\bullet}]$ (transition 4) which can be accompanied by the emission of light. The ultimate electron donor to $Y_Z^{+\bullet}$ is H_2O.

Thus, the hypothesis, which suggests inhibition of the photochemical quenching of excitation energy during reduction of Q_A (Duysens and Sweers, 1963) leads to relations (4a) and (4b). Furthermore, the model considers F_V as prompt fluorescence (see also: Kitajima and Butler, 1975).

However, this model cannot explain the following: according to the equation (4b), complete blockage of the photochemical reaction, having a quantum yield of $\varphi_p \geq 98\%$ should lead to an increase of fluorescence intensity by a factor of ~50. Nevertheless, experimentally 4-5-fold increase of chlorophyll fluorescence is observed (Klimov et al., 1977), which questioned this approach for explanation of the mechanism of the increase of chlorophyll fluorescence (or appearance of variable fluorescence).

Klimov's recombination luminescence. According to the Duysens hypothesis (Duysens and Sweers, 1963), chlorophyll fluorescence in the presence of both oxidized (F_0), or reduced plastoquinone Q_A (F_M) in the PSII reaction center have the same nature, i.e., they are represented by prompt fluorescence emitted at the same time range. However, it has been shown experimentally that the part of fluorescence emitted from the so-called "closed" centers ($[P_{680}Pheo]Q_A^{-\bullet}$ state) has a lifetime in the nanosecond range. In different studies, the lifetime of 2-4 ns was reported for the slow component of chlorophyll fluorescence (Klimov et al., 1978; Haehnel et al., 1982; 1983; Nairn et al., 1982; Karukstis and Sauer, 1985; Mauzerall, 1985; Holzwarth et al., 1985; Holzwarth, 1986; Moya et al., 1986). The appearance of the slow component of chlorophyll fluorescence after the reduction of plastoquinone Q_A, also contradicts the above-mentioned Duysens hypothesis.

A more attractive mechanism explaining the increase of chlorophyll fluorescence upon reduction of Q_A is a model proposed by Klimov (Klimov et al., 1978; see also: Klevanik et al., 1991). Unlike the above hypothesis, this model considers functionality of the photochemical pathway of utilization of the excitation energy in the PSII reaction centers after reduction of Q_A. According to the model, an increase of chlorophyll fluorescence when Q_A becomes reduced, i.e. induction of the variable fluorescence of chlorophyll may occur in the following way: the transformation of the energy starts with the excitation of the primary electron donor P_{680} (P_{680}*) and subsequent fast (for ~ 3 ps) electron

transfer from the excited P_{680}* to the pheophytin molecule, which leads to the formation of the unstable [$P_{680}^{+\bullet}Pheo^{-\bullet}$] pair (Klimov et al., 1977; Wasielevski et al., 1989a; 1989b; Hasting et al., 1992; Schelvis et al., 1994; Visser et al., 1995). According to other authors, for the formation of the [$P_{680}^{+\bullet}Pheo^{-\bullet}$] pair 8 ps are required (Greenfield et al., 1997). Stabilization of the [$P_{680}^{+\bullet}Pheo^{-\bullet}$] pair occurs due to electron transfer from $Pheo^{-\bullet}$ to plastoquinone Q_A for ~ 200 ps (Nuijs et al., 1986; Eckert et al., 1988; Leibl et al., 1989) and the reduction of $P_{680}^{+\bullet}$ by the electron transferred from tyrosine Y_Z for 20-260 ns (Brettel et al 1984, Sclodder et al., 1984; Meyer et al., 1989). When Q_A is reduced photochemically, stabilization of the [$P_{680}^{+\bullet}Pheo^{-\bullet}$] pair may occur as a result of charge recombination between $P_{680}^{+\bullet}$ and $Pheo^{-\bullet}$ (Klimov et al., 1978; Klevanik et al., 1991), which proceeds in the time scale of 2-30 ns depending on the molecular size of PSII preparation used in the study (Shuvalov et al., 1980; Danielius et al., 1987; Hansson et al., 1998). The decay of the [$P_{680}^{+\bullet}Pheo^{-\bullet}$] state due to charge recombination can occur through the excited state of P_{680}* (Fig. 1, b). In this case, conversion of P_{680}* to the ground state is accompanied by the emission of light quanta, which represents the variable fluorescence of chlorophyll (Klimov et al., 1978; Klimov and Krasnovskii, 1981; Klevanik et al., 1991).

Thus, the hypothesis includes a molecular mechanism. According to this hypothesis, the variable fluorescence is a delayed luminescence emitted during charge recombination in the PSII reaction center.

2.3. Fluorescence of chlorophyll is a loss of excitation energy

Being part of the excitation energy of antenna pigments, which cannot be utilized by the PSII reaction centers, chlorophyll fluorescence represents a loss of excitation energy. As shown above, it comprises ~2% (2-5%, Kitajima and Butler, 1975) of the excitation energy of the antenna. Since F_0 is emitted by the "open" centers at low intensity of excitation light when the energy transfer to the PSII reaction center balances with electron transfer events in reaction centers from P_{680} to plastoquinones Q_A, Q_B and further. In the case of maximal (or variable) fluorescence of chlorophyll, differences in the rate of electron transfer from P_{680} to plastoquinone Q_A (~ 200 ps: Nuijs et al., 1986, Eckert et al., 1988; Leibl et al., 1989), and from $Q_A^{-\bullet}$ to plastoquinone Q_B (100-200 μs: Bowes and Crofts, 1980; Crofts and Wraight, 1983; Robinson and Crofts, 1983; De Wijn and van Gorkom, 2001) leads to the accumulation (increase in the quasi-stationary concentration) of $Q_A^{-\bullet}$ in the PSII reaction centers under strong excitation ("actinic") light. In this circumstance only a part of the separated charges is stabilized through the charge recombination, during which the energy of the redox pair [$P_{680}^{+\bullet}Pheo^{-\bullet}$] may be lost as a luminescence. However, a part of the separated charges is involved in maintaining the electron transfer along the redox chain, thereby performing photosynthesis. Thus, in this sense, the concept of "closed" centers becomes meaningless.

Nevertheless, the variable fluorescence is closely related to the processes of electron transfer from water to plastoquinones, and therefore its intensity can be tuned by the factors affecting the electron transfer in PSII from the P_{680} to Q_A (in the reaction center), from H_2O to $P_{680}^{+\bullet}$, and from $Q_A^{-\bullet}$ to Q_B. Thus, the variable fluorescence of chlorophyll may be successfully applied to the study of the photosynthetic apparatus, and to the study of the problems of plant physiology.

2.4. "Maximum quantum efficiency" of photosystem II

Chlorophyll *a* in oxygenic species represents an intrinsic fluorescence probe. Considering the complex response against different external factors, chlorophyll fluorescence is widely used in various fields of plant biology. As mentioned above, about 20 different parameters (amplitude, kinetic and derivatives) characterizing complex changes of chlorophyll fluorescence were reported by different authors in the literature (Kromkamp and Forster 2003, Baker, 2008, Brestic and Zivcak, 2013). Among these parameters, a particular interest represents "maximum quantum efficiency" of PSII, determined on the basis of the F_0, F_V and F_M.

The "maximum quantum efficiency" of photosystem II, denoted sometimes as "maximum quantum yield" or "potential quantum yield", is defined by the ratio of variable and maximum fluorescence of chlorophyll:

$$Y = \frac{F_M - F_0}{F_M} = \frac{F_V}{F_M} \quad (5)$$

Usually the parameter Y (**Y**ield) is determined in the dark-adapted leaves, and used as an indicator of the photochemical activity of the plant photosynthetic apparatus thereby the physiological state of the plants. It is considered as the most sensitive indicator characterizing the effects of different stresses on plants. For most plants grown under non-stressed conditions, the maximum measured value of *Y* is 0.83 (Björkman and Demmig, 1987). Under stressful conditions, usually a significant decrease in this value is observed. Using Y and its characteristic terminology, many authors disregard the mechanisms of photosystem II during the studies, which in turn may lead to misinterpretation of the results. Indeed, according to the expressions 4b and 5 when the value F_M/F_0 is equal to 5.0, the quantum yield of photochemistry (φ_p) is 0.8, and this result may be perceived as a true result. However, this seeming "success" arises from the mechanistic assumption used in deriving equation 4b (see also below, point 4). Thus, when using the parameters F_V, F_M and Y for the estimation of photochemical processes and the PSII state, the following comments should be considered as useful:

1) Chlorophyll fluorescence F_0, F_V, and maximal fluorescence F_M refer to the loss of excitation energy in photosystem II. The ratio of the values of these two radiative losses (F_V/F_M) cannot be used as an indicator of the quantum yield (efficiency) of photosystem II, i.e. photochemical electron transport in PSII.

2) Quantum yield of chlorophyll fluorescence does not represent the quantum yield of photochemical electron transfer in PSII. Identifying the quantum yields of the photochemical reaction and chlorophyll fluorescence, can lead to the errors during interpretation of the results. In photosynthetic systems under constant illumination, the quantum yield of chlorophyll fluorescence is ~ 2% (2-5% in: Kitajima and Butler, 1975), and it consists of the sum of F_0 and F_V. Therefore, the ratio of the parameters, which total values (2-5%) are far from the quantum yield of photochemistry (≥95%), cannot be used as an indicator of the quantum yield of photosystem II.

3) Above (paragraph 2.1-2.3) it was shown that the constant (F_0) and the variable fluorescence of the chlorophyll F_V include different mechanisms: F_0 is emitted directly by the antenna before the excitation energy reaches the RC, and F_V is emitted by the antenna through the processes occurring in RC. Maximum fluorescence (F_M) includes F_0 ($F_M = F_0+F_V$). Therefore, the "maximum quantum efficiency" of photosystem II estimated by the F_V/F_M ratio will lead to incorrect results. This can be confirmed by simple examples:

a) In plants, which are not subjected to stress, the value of F_V/F_M is ~0.8 (Klimov et al., 1977; Björkman and Demmig, 1987). However, according to expression 5, a twofold (50%) decrease in the intensity of the variable fluorescence of chlorophyll at a constant F_0 results in F_V/F_M value of ~0.66 (~80% of the maximum Y), the correctness of the use of the parameter Y as an indicator and for evaluating the stress of plants may cause doubts.

b) Inhibition of the donor side of photosystem II, for example, when Mn cluster is removed, leads to the decreases in F_V almost to zero (Klimov et al., 1982). According to equation 5, in this case the "maximum quantum efficiency" of PSII should also decrease to zero. However, it was experimentally found that in this case the photochemical activity of the PSII reaction center, thus the quantum yield of photosystem II remains high.

4) Another reason pointing to the incorrectness of using F_V/F_M to determine the "maximum quantum efficiency" of PSII is that this approach includes the mechanisms proposed by Duysens and Sweers (1963), which accept the concept of "closed" PSII centers and cannot explain the RC mechanisms properly. However, as shown above (Klimov et al., 1978, Klevanik et al., 1991), the PSII reaction centers remain open when Q_A is reduced. In this case, part of the redox energy stored in the RC is consumed photosynthetically, and only a small part of the energy can be lost in the form of luminescence.

5) During the determination of quantum efficiency using the above method, it is impossible to obtain detailed information about the sites and mechanisms of inhibition of the photosynthetic electron transport chain of plants under stressfull conditions. However, F_V itself carries information about photoinduced electron transfer in photosystem II, from water to plastoquinones. When using suspensions, combining with other available met-

hods, it is relatively easy to identify the mechanism of inhibition. In addition, in suspensions, it is possible to equalize the concentration of chlorophyll accurately, which allows, without difficulty, comparing the F_V values of each individual measurement.

3. Conclusion

One of the main properties of photosystem II is the emission of light by chlorophyll *a* in this complex, which provides properties of a fluorescent marker in the study of the physiological state of plants, algae and cyanobacteria. Under continuous illumination, and due to the processes that are not directly related to photosynthesis, the intensity of chlorophyll fluorescence changes in a very complex manner, which allows widespread using of chlorophyll fluorescence in studies of oxygenic species. Among the fluorescence components of F_0, F_V, and the parameter "maximum quantum efficiency", a variable fluorescence of chlorophyll is the most suitable parameter characterizing the state of the photosynthetic apparatus. Despite the fluorescence of chlorophyll is the loss of the absorbed light energy, due to the close relationship between the processes occurring in the PSII reaction centers (growth kinetics of F_V and its amplitude are related to the processes of electron transfer to plastoquinone Q_A and charge recombination in the RC, respectively), F_V may be considered as a more appropriate component of fluorescence in studies of the physiological state of oxygenic species. Changes in its intensity can be easily interpreted upon the influence of different factors on photosystem II in isolated chloroplasts and PSII membranes. However, when plant leaves are being examined, evaluation and comparison of the results of each individual measurement is difficult and requires special attention. Another component of chlorophyll fluorescence, F_0 is not directly related to RC processes. However, this component of fluorescence can be used as an important indicator in stressful situations, for example, due to changes in membrane fluidity under high temperature stress, or during the study of the antenna systems (Yamane et al., 1997). It was mentioned above that the parameter "maximum quantum efficiency" of PSII (parameter Y) is not a true quantum yield and, thus may incorrectly describe the state of the photosynthetic apparatus. The Y concept is based on the concepts of Duysens and Sweers (1963), and Kitajima and Butler (1975) and does not reflect the molecular processes occurring in the photosynthetic apparatus. However, the use of the ratio F_V/F_M without attributing it the name "maximum quantum efficiency", can play an auxiliary role in estimating the photochemical activity of photosystem II. Whereas, the ratio F_V/F_0, representing relative share of two different processes occurring in the PSII reaction centers and in the antenna, which contributes to the chlorophyll fluorescence can be more suitable for characterizing the photosynthetic apparatus.

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Xlorofil fluoressensiyası və fotosistem II-nin "maksimal kvant effektivliyi" parametrinin bitki tədqiqatlarında istifadəsi

Y.M. Feyziyev

AMEA Molekulyar Biologiya və Biotexnologiyalar İnstitutu

Xlorofilin fluoressensiyası və onun dəyişmələri bitki, birhüceyrəli yosun və sianobakteriyalarda fotosistem II kompleksinin (FSII) fəaliyyətinin indikatoru olaraq geniş istifadə olunur. İndiyədək ədəbiyyatda xlorofilin fluoressensiyasını xarakterizə edən 20-dək parametr məlumdur. Bu işdə FSII fluoressensiyanın bəzi əsas xarakteristikaları – xlorofilin başlanğıc (F_0), maksimal (F_M) və dəyişən fluoressensiyaları (F_V) müqayısə olunmuş, eləcə də FSII-nin maksimal kvant effektivliyi adlanan törəmə $(F_M-F_0)/F_M$ parametrinin критик təhlili aparılmışdır. FSII reaksiya mərkəzi proseslərinin və dəyişən fluoressensiyanın təsvirində istifadə olunan Duysens (Duysens and Sweers, 1963) hipotezi və Klimov tərəfindən irəli sürülmüş rekombinasiya lüminessensiyası hipotezinin (Klimov et al., 1978) qısa, müqayisəli təhlili aparılmış və oksigenli fotosintezdə aparılan fluoressensiya ölçülərinin nəticələrinin interpretasiyasınnın çatışmazlıqları müzakirə olunmuşdur. Bitki fiziologiyası və ekofizioloji tədqiqatlarda geniş istifadə olunan FSII-nin "maksimal kvant effektivliyi" parametrinin tətbiqindəki qeyri-dəqiqliklər göstərilmişdir.

Açar sözlər: *Fotosistem II, xlorofilin fluoressensiyası, maximum kvant effektivliyi*

Флуоресценция хлорофилла и «максимальная квантовая эффективность» фотосистемы II в исследованиях растений

Я.М. Фейзиев

Институт молекулярной биологии и биотехнологий НАН Азербайджана

Флуоресценция хлорофилла *a* широко используется в качестве индикатора состояния_фотосистемы II (ФСII) растений, водорослей и цианобактерий. В литературе разными авторами сообщались о 20-и разных параметрах флуоресценции хлорофилла ФСII. В данной работе обсуждены три из этих характеристик: начальная (F_0), максимальная (F_M) и переменная флуоресценция хлорофилла (F_V) и производная величина (F_M-F_0)/F_M, называемая «максимальной квантовой эффективностью» ФСII. Осуществлен краткий и сравнительный анализ гипотезы Дейзенса (1963) и гипотезы рекомбинационной люминесценции Климова (Klimov et al., 1978), применяемых для описания процессов реакционного центра ФСII, и обсуждены возможные ошибки, допущенные в интерпретациях переменной флуоресценции хлорофилла. Обсуждены возможные неточности при применении параметра «максимальной квантовой эффективности» PSII используемой для оценки активности фотосинтетического аппарата и физиологического состояния растений.

Ключевые слова: *Фотосистема II, флуоресценция хлорофилла, максимальная квантовая эффективность*